



The control of growth and differentiation of the wing imaginal disks of *Manduca sexta*

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Abstract

During the larval feeding period, the growth of the wing imaginal disks of Lepidoptera is dependent on continuous feeding. Feeding and nutrition exert their effect via the secretion of bombyxin, the lepidopteran insulin-like hormone. When larvae stop feeding and enter the wandering stage in preparation for metamorphosis, the control of imaginal disk growth becomes feeding and nutrition-independent. Growth of the wing imaginal disks of non-feeding wandering stage *Manduca sexta* can be stopped by removal of the brain, indicating that a brain-derived factor is required for continued disk growth. Isolated wing disk growth *in vitro* requires both 20-hydroxyecdysone (20E) and either brain extract or bombyxin to achieve normal growth. *In vitro*, brain extracts and synthetic bombyxin have little or no effect in stimulating disk growth, but they greatly enhance the effect of 20E, indicating that 20E and bombyxin act synergistically to modulate growth of the imaginal disk. Brain extract and bombyxin induce a suite of insulin-response events in cultured wing disks, which indicate that bombyxin and 20E act through separate and synergistic pathways. The dose-response to 20E reaches a plateau at about 0.1 µg/ml. Tracheal differentiation of the wing disks can be induced to initiate *in vitro* by a low concentration of 20E, whereas higher concentrations of 20E only stimulate growth.

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Introduction

The wing imaginal disks of Lepidoptera grow continuously and exponentially throughout the late larval and prepupal periods (Miner et al., 2000; and this paper). During the larval feeding phase, growth of the wing disk depends on nutrition. When a larva is starved, imaginal disk growth ceases within a few hours (Miner et al., 2000; Nijhout and Grunert, 2002; A. Tobler, unpublished results). Likewise, if a larva is fed on a diet of low nutritive value, larval growth rate is slow and so is the growth rate of the imaginal disk. During the feeding phase, growth of the wing imaginal disks is modulated to remain in proportion to the growth of the rest of the body.

Studies in *Bombyx mori* have shown that nutrition regulates the secretion of bombyxin, the lepidopteran insulin. Starvation of *Bombyx* larvae causes a decline in the level of bombyxin in the blood, and injection of glucose stimulates bombyxin secretion (Satake et al., 1997; Masumura et al., 2000). Bombyxin could therefore be an indicator of the nutritional state of the insect. In *Drosophila*, insulin-like proteins are also involved in the regulation of nutrient-dependent growth (Looveren and Hafen, 2004; Edgar and Nijhout, 2004).

Studies with isolated imaginal disks have revealed the conditions required for normal growth. When wing imaginal disks taken from feeding and growing last-instar larvae of *Protoparce coenra* are placed in a nutrient-rich culture medium they fail to grow. Such cultured disks can, however, be made to grow at their normal rate by adding bombyxin and a low optimal concentration of the steroid molting hormone 20-hydroxyecdysone (20E) to the culture medium (Nijhout and Grunert, 2002; see also Kawasaki, 1988).

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